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Multiple breeding in the Great Tit, II. The costs of rearing a second clutch

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Summary

1. Multiple breeding (raising more than one batch of young per breeding season) is a common life-history tactic, but little is known as yet of the accompanying costs and benefits. Second clutches of Great Tits, a facultative multiple breeder, were removed over three years to investigate the costs of rearing a second clutch.

2. Female parents, but not males, survived significantly better than unmanipulated control birds when the second clutch was removed. The difference between the sexes indicates a potential sexual conflict over the decision to start a second clutch. In neither sex were effects found on egg production in the next year. However, birds of both sexes produced more fledglings from first clutches in the following year when the second clutch had been removed.

3. In males, the experimental effect on fledgling production in the next year could be attributed to their mates, because this effect was restricted to males that bred with the same female as in the previous year. In females, this effect was also found among birds that bred with a new mate, which suggests that rearing a second clutch had a long-term effect. Females, but not males, found roosting in the following winter had lower mass when the second clutch had been removed, which supports the conclusion that rearing a second clutch has long-term effects.

4. The experimental effect on female survival was found in two winters with low food availability, but not in a winter with high food availability. This is in agreement with the results of a non-experimental analysis of data collected in the same population. The effect on fledgling production in the next year was also restricted to years with low food availability in the intervening winter. This suggests that the costs of rearing a second clutch depend on food availability in winter. The possibility that the costs of reproduction generally depend on environmental quality and possible mechanisms are discussed.

5. Food availability in winter is probably unpredictable at the time second clutches are started, and therefore Great Tits should 'bet-hedge' with regard to the decision to start a second clutch.

Key-words: Bet-hedging, costs of reproduction, energy reserves, multiple breeding, *Parus major*, sexual conflict

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Introduction

Multiple breeding, the completion of more than one reproductive cycle within a breeding season, is a common reproductive strategy in a variety of taxa (Verhulst, Tinbergen & Daan 1997). Life-history theory predicts that differentiation among species in single and multiple breeders, as well as the fine tuning of reproductive decisions within multiple breeders, can be understood as the outcome of an optimization process, or in other words, in terms of costs and benefits (Lessells 1991; Roff 1992; Stearns 1992). This implies animals should rear the number of clutches that maximizes their fitness, where fitness includes both the reproductive value of the clutches produced

in a given year and the residual reproductive value of clutches produced in later years.

Little is known as yet of the costs of multiple breeding. Bryant (1979) studied House Martins *Delichon urbica* and found that females that reared two broods had significantly lower survival rates than single-brooded females, which suggests a cost of reproduction. Dobson (1990) showed that multiple-breeding bird species had lower survival rates, as compared with species rearing only one brood per season, which also suggests a cost of multiple breeding. However, other causes cannot be ruled out. For example, it is possible that females that started a second clutch were individuals expecting a lower return rate anyway, and therefore

made a larger investment. Under such circumstances a negative correlation between reproductive effort and residual reproductive value cannot be considered evidence for costs of reproduction.

Tinbergen, van Balen & van Eck (1985) analysed variation between years in mean survival rates of Great Tits *Parus major* breeding on Vlieland, and showed that adult survival was negatively correlated with the production of fledglings among years with low food availability in winter, but not among years with high food availability. Variation between years in fledgling production was largely due to variation in the occurrence of multiple breeding (J. M. Tinbergen, personal communication), which suggests that this relationship may reflect the costs of rearing a second clutch. However, Den Boer-Hazenwinkel (1987) compared survival rates of single-brooded and multiple-brooded birds within years in two other populations of Great Tit, and, in contrast to the results of Tinbergen *et al.* (1985), she found that multiple breeding was associated with *higher* survival rate. A similar result was obtained by Winkel & Winkel (1995) in a study of the Coal Tit *Parus ater*.

Both positive and negative correlations between natural variation in fledgling production and parental survival can potentially be attributed to differences in quality between birds, and therefore an experimental approach is required. In this paper the results of phenotypic manipulations that were carried out to measure the costs of rearing a second clutch in the Great Tit are reported. The experiment consisted of the removal of the second clutch. Subsequently survival and future reproductive success of control and experimental birds were compared.

The experiment was carried out over 3 years, and food availability in winter varied among years. The experimental data can therefore also be used to evaluate whether the interaction between the production of young and the availability of food in winter with respect to the survival rate of breeding birds, as reported by Tinbergen *et al.* (1985), is a causal relationship.

In Great Tits manipulation of the number of young in the first brood affects the occurrence of second clutches: when the size of the first brood is reduced, more pairs start a second clutch (Tinbergen 1987; Smith, Källander & Nilsson 1987; Lindén 1988; Verhulst 1995). This suggests that for pairs with a reduced brood size the benefits of a second clutch are higher and/or the costs of rearing a second clutch are lower. If the costs of rearing a second clutch depend on brood size of the first brood, we would expect the experimental removal of second clutches to have a larger effect on the future reproductive output of birds of which the first clutch was enlarged than on birds of which the first brood was reduced in size. Clutch size of first clutches was experimentally reduced in two of the three experimental years, and whether the effect of the clutch removal on residual reproductive value depended on the manipulation of the first clutch was evaluated.

Methods

Experiments were carried out on Vlieland, an island in the Dutch Waddensea, over three years (1988, 1990 and 1991). Dyads of second clutches were selected with approximately equal laying date and clutch size, and in each dyad one randomly chosen clutch was removed shortly before hatching. In 1990 and 1991, first clutches of pairs involved in the removal experiment were either an (unmanipulated) control clutch or a clutch of which the number of eggs was experimentally reduced by 50%. Within each dyad (for the removal experiment) both pairs had the same treatment with regard to their corresponding first clutches. Further details regarding the study area, the experimental protocol, the collection of breeding data and data analysis are presented in a companion paper (Verhulst *et al.* 1997).

Local survival of breeding birds was measured by nightly checks of nestboxes in winter, by capturing breeding birds in the next year and observations of non-breeding birds in the breeding season. Nightly checks of nestboxes were carried out once in the first half of December in each winter. Roosting birds were identified by their numbered rings and then weighed (to the nearest 0.1 g) and tarsus length was measured (to the nearest 0.1 mm).

Seed production was not measured on Vlieland and therefore measurements of the beech crop in the Hoge Veluwe study area (van Balen 1980) were used as a measure of food availability in winter. This is reasonable because the beech-crop index correlates with the survival of adult Great Tits on Vlieland, despite the fact that beeches are almost absent on Vlieland (Tinbergen *et al.* 1985). Furthermore, seed formation of beeches *Fagus sylvaticus* is synchronized between trees over large areas (Perrins 1966; J. H. van Balen, personal communication), and the beech crop index is strongly correlated with the seed crop of other tree species, such as birch *Betula* spp. and Black Elder *Alnus glutinosa*, which do occur on Vlieland.

Results

In total there were 57 dyads of control and experimental pairs ($N = 20$, 19 and 18 dyads in 1988, 1990 and 1991; respectively). Control and experimental pairs did not differ in distribution over the different woods, laying date and clutch size of the second clutch, or hatching date, number of fledglings and nestling mass of the corresponding first clutches of pairs included in the removal experiment (data and tests are presented in a companion paper: Verhulst *et al.* 1997).

In each year some pairs produced a replacement clutch following removal of the second clutch. The annual survival of females that laid a replacement clutch (0.46, $n = 13$) was slightly lower than the survival of females that did not lay a replacement clutch (0.68, $n = 44$), but this difference was not significant

(logistic regression, controlling for year, $F_{1,53} = 1.8$, $P > 0.1$). Survival of males with which the female laid a replacement clutch was slightly higher (0.62, $n = 13$) than survival of males with which the female did not lay a replacement clutch (0.52, $n = 44$), but this difference was not significant (logistic regression, controlling for year, $F_{1,53} = 0.01$, $P > 0.9$). Hence data of pairs with and without a replacement clutch were pooled.

SURVIVAL AND PROPORTION BREEDING IN THE NEXT YEAR

The effect of the experiment on local survival until the next breeding season was evaluated. When years were pooled (Fig. 1), removal of the second clutch significantly enhanced survival of females ($\chi^2 = 4.3$, $df = 1$, $P < 0.05$), but male survival was not affected ($\chi^2 = 0.04$, $df = 1$, $P > 0.8$).

As a next step the effect of the experiment on subsequent reproduction was evaluated. Some birds were recorded to be alive in the next breeding season without producing any eggs. Females sometimes incubated empty nests, but the probability that a female was incubating an empty nest was not affected by the experiment (8% of control females ($n = 25$), 13% of

experimental females ($n = 32$), $\chi^2 = 0.3$, $df = 1$, $P > 0.5$). Males could be either mated to a female that incubated an empty nest or be without a partner. Also among males there was no effect of the experiment on the probability of being without eggs (31% of control males ($n = 29$), 27% of experimental males ($n = 30$), $\chi^2 = 0.1$, $df = 1$, $P > 0.7$).

CLUTCH SIZE AND FLEDGLING PRODUCTION IN THE NEXT YEAR

The effect of the experiment on clutch size and reproductive success of the first clutch was further evaluated for birds that did produce eggs. Clutch size in the next year did not differ significantly between control and experimental birds of either sex (Table 1; two sample t -test, $P > 0.6$). Controlling for year, manipulation of the first clutch, change in laying date and/or clutch size of the first clutch in the year of the experiment did not change this result.

The effect of the experiment on reproductive success of first clutches in the next year was evaluated. In all three years there were experiments with first clutches in the following year (Verhulst 1995), and manipulated clutches were excluded from this analysis. Females whose second clutch was removed fledged on average 4.0 more young from their first clutches in the next year (Fig. 2; Table 1; $F_{1,21} = 11.6$, $P < 0.003$). The experimental effect was not due to an effect on clutch size (Table 1), but could be attributed to an effect on fledging success (the proportion of eggs resulting in a fledged young). Fledging success in the next year was significantly higher when the second clutch had been removed ($F_{1,21} = 7.9$, $P < 0.02$). Further analysis suggested that this effect could largely be attributed to an effect on nestling survival (control, $\bar{x} \pm \text{SD} = 0.55 \pm 0.21$, $n = 6$; experimental, $\bar{x} \pm \text{SD} = 0.81 \pm 0.21$, $n = 13$; $F_{1,18} = 5.2$, $P < 0.05$), and to a lesser extent to an effect on hatching success (control, $\bar{x} \pm \text{SD} = 0.66 \pm 0.43$, $n = 8$; experimental, $\bar{x} \pm \text{SD} = 0.92 \pm 0.27$, $n = 14$; $F_{1,18} = 5.2$, $P < 0.05$).

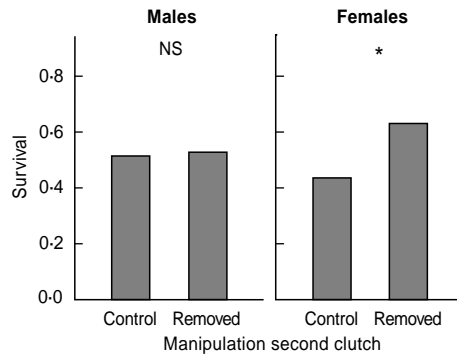


Fig. 1. Survival of control and experimental birds until the next breeding season. Years pooled. $N = 57$ for each bar. NS not significant, * $P < 0.05$.

Table 1. Manipulation of the second clutch and parental survival until the next breeding season and reproductive parameters of first clutches in the next year (clutch size, fledging success (proportion of eggs resulting in a fledged young) and number of fledglings). Only nests in which eggs were laid which were not experimentally manipulated in the next year were used in the calculation of fledging success and the number of fledglings

Experimental category		Females											Males												
		Survival			Clutch size			Fledging success			Number of fledglings			Survival			Clutch size			Fledging success			Number of fledglings		
		\bar{x}	n		\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	n	\bar{x}	SD	n	\bar{x}	SD	n	\bar{x}	SD	n	
1988	Control	0.35	20	7.6	1.8	5	0.35	0.38	3	3.0	3.0	3	0.35	20	8.3	2.5	3	0.37	0.38	3	3.3	3.1	3		
	Removed	0.65	20	9.1	1.3	7	0.82	0.13	3	7.7	2.1	3	0.30	20	9.3	1.7	4	0.91	–	1	10	–	1		
1990	Control	0.47	19	9.3	1.5	9	0.45	0.27	3	4.0	2.0	3	0.58	19	9.0	1.4	9	0.21	0.26	3	1.7	2.1	3		
	Removed	0.47	19	8.4	1.5	8	0.59	0.46	5	4.4	3.5	5	0.68	19	8.6	1.7	9	0.53	0.45	6	4.2	3.7	6		
1991	Control	0.50	18	9.3	1.7	9	0.19	0.33	3	1.3	2.3	3	0.61	18	9.0	0.8	7	0.53	0.45	6	4.2	3.7	6		
	Removed	0.78	18	9.6	1.1	13	0.83	0.12	6	8.3	1.4	6	0.61	18	9.0	1.1	9	0.79	0.07	4	7.5	0.6	4		

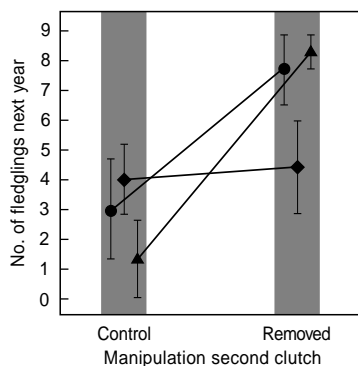


Fig. 2. Number of fledglings (± 1 SE) from first clutches in the year after the experiment (● 1988; ◆ 1990; ▲ 1991) for females. Only females that produced eggs in the next year and whose clutch was not manipulated were included.

Males whose second clutch was experimentally removed fledged about three more young from first clutches in the next year (controlling for year: $F_{1,17} = 6.1$, $P < 0.025$). As clutch size in the next year was not affected (Table 1), it could be expected that the effect would be due to an effect on fledgling success. The experimental effect on fledgling success in the next year approached significance (controlling for year: $F_{1,17} = 3.9$, $P < 0.07$).

Thus both males and females fledged fewer young from first clutches in the next year when they were allowed to rear the second clutch. However, these comparisons are not independent because surviving pairs may still be mated in the next season. Therefore the effect of the experiment on fledgling production was investigated separately for birds that retained their mate, and birds paired with another bird as in the year of the experiment. In the subset of pairs that remained paired the experimental pairs produced more fledglings (from first clutches) in the next year ($P < 0.025$). Similarly, among females that changed partner between years (either through divorce or death of the male) the clutch removal significantly increased fledgling production ($P < 0.05$). However, among males that changed partner there was no significant

effect of clutch removal on fledgling production ($P > 0.5$). This suggests that the experimental effect on fledgling production in males can be attributed to their partners, not to the males themselves.

FOOD AVAILABILITY IN WINTER

The effect of food availability in winter on the costs of rearing a second clutch was further evaluated. The experiment affected female survival, but not male survival, and therefore this analysis was limited to the females.

The years 1988 and 1991 were followed by a winter with a low beech crop (0 full nuts per m^2 in both winters) and 1990 was followed by a winter with a large beech crop (683 full nuts per m^2 , the highest value since 1976; J. H. van Balen and J. M. Tinbergen, personal communication). Thus it can be predicted on the basis of the results of Tinbergen *et al.* (1985) that the effect of the experiment should be stronger in 1988 and 1991 (low food) as compared with 1990 (high food). In accordance with this prediction, the experiment had no effect in the year with high food availability ($\chi^2 = 0.0$, $df = 1$, $P = 1.0$), but in the years with low food availability survival of experimental females was 30% higher (Fig. 3 1988 and 1991 pooled: $\chi^2 = 6.5$, $df = 1$, $P = 0.01$).

The interaction between food availability and the experimental effect was tested directly in a log linear analysis (Sokal & Rohlf 1994). Significance of the three-way interaction term between experimental category, food availability and survival was tested by dropping this term from the saturated model. A one-sided P -value is used because of the specific prediction that is being tested. The interaction term between food availability and experiment approached significance (maximum likelihood $\chi^2 = 2.3$, $df = 1$, $P < 0.07$).

As shown above, experimental females produced more fledglings from first clutches in the next year. This effect was also dependent on food availability in winter (experiment \times food availability interaction: $F_{1,19} = 6.6$, $P < 0.02$), the effect being smaller in the year with high food availability in winter (Fig. 2; Table 1). In males, the interaction between the experiment and food availability in winter was not significant ($F_{1,17} = 0.4$, $P > 0.5$).

Although it was shown that the removal of the second clutch enhanced survival of females, but not of males, this is not sufficient to conclude that the experimental effect differs between the sexes. Therefore the interaction term between experimental category, sex and survival was tested in a log linear analysis, using only the data from the two years with low food availability in winter. The experimental effect on survival differs significantly between the sexes (maximum likelihood $\chi^2 = 4.0$, $df = 1$, $P < 0.05$). This is an interesting result, because both parents feed their second brood nestlings at the same rate (paired t -test, $P = 0.3$, $n = 24$ broods observed on day 12 in 1992; N. Verboven, personal

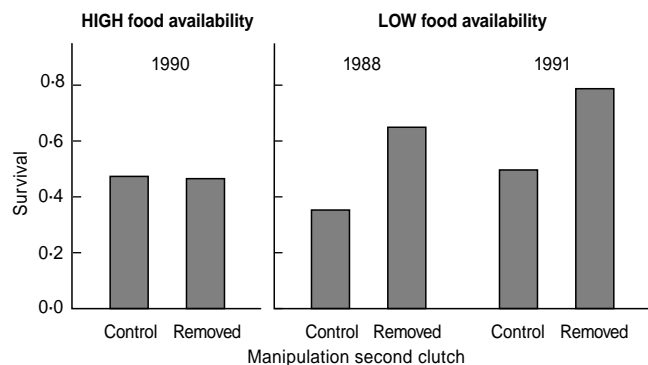


Fig. 3. Survival of control and experimental females until the next breeding season in (a) a year with high food availability in winter (1990) and (b) two years with low food availability in winter (1988, 1991).

communication), suggesting either reduced investment by the male at a later stage, or a differential effect of reproductive effort on the residual reproductive value.

EFFECTS OF SIZE OF THE FIRST CLUTCH

Does the effect of the clutch removal on survival and fledgling production depend on (experimentally manipulated) brood size of the first clutch? In 1990 and 1991 pairs with a second clutch had an unmanipulated or an experimentally reduced first clutch. However, only in 1991, a year with low food availability in winter, did clutch removal affect female survival (Fig. 3). Therefore, the interaction between clutch size manipulation of the first clutch and experimental removal of the second clutch was investigated for 1991 only, which reduced sample size to 36 females in four experimental categories.

There was a tendency for the experimental removal of the second clutch to have a stronger effect on survival of females of which the first clutch was experimentally reduced (control, 5/10 survived; removed, 9/10 survived) than among females of which the first clutch was unmanipulated (control, 4/8 survived; removed, 5/8 survived), but in a log linear analysis the interaction was not significant (maximum likelihood $\chi^2 = 1.2$, $df = 1$, $P > 0.2$) and, if anything, opposite to the expectation that the costs of rearing a second clutch would be lower for pairs of which the first clutch had been experimentally reduced (see Introduction).

Analysis of the effect of clutch-size manipulation of the first clutch on fledgling production in the next year yielded the same result. In a multiple regression analysis the manipulation of the first clutch was not significantly correlated with female fledgling production in first clutches in the next year when manipulation of the second clutch was controlled for. This was tested for all years combined (treating all first clutches in 1988 as control clutches), for 1990 and 1991 combined and for 1991 only ($P > 0.4$ in all comparisons). The interaction between manipulation of the first and the second clutch was also not significant in a similar analysis ($P > 0.3$ in all comparisons).

WHEN DOES THE EXPERIMENTAL EFFECT OCCUR?

As a step towards identifying the mechanism causing the variation in female survival rate between experimental categories it was investigated at what stage in the seasonal cycle the experimental effect became apparent. Two time intervals were distinguished: from the breeding season until winter (December and January), and from winter until the next breeding season (15 April until 1 August). Recapture rate in a given period is the product of survival rate until that period and capture probability in that period. The intensity of field work in the breeding season was high and therefore the capture probability was assumed to

be 1. Capture probability in winter was estimated from the data and was taken to be the proportion of birds that survived until the next breeding season that was also captured in winter. Capture probability in winter of control (0.76, $n = 25$) and experimental females (0.75, $n = 36$) was very similar, but capture probability varied slightly between years. Therefore one estimate was made for each year.

In the year with high food availability in winter, survival of control and experimental females was similar in both time intervals (Fig. 4a). In the years with low food availability, survival of experimental females appears to be higher all through the year (Fig. 4b). The differences in survival rate were not significant in either period but the results should be interpreted in the light of the results presented above (Fig. 3) which showed that survival from one breeding season to the next was significantly enhanced by the removal experiment. These results suggest that clutch removal had a long-term effect on the phenotypic and/or environmental quality of the females.

BODY MASS IN WINTER

Data of body mass of birds found roosting in winter were analysed (Table 2), to investigate further if the experiment had a long-term effect on the birds. In a multiple regression analysis the effects of year (as a factor), sex, tarsus length, time of weighing, and manipulation of the first and the second clutch were studied. Control and experimental birds did not differ significantly in tarsus length (both sexes: $P > 0.3$) or time of weighing (both sexes: $P > 0.5$). Time of weighing and manipulation of the first clutch did not significantly correlate with mass and were therefore excluded from the analysis that is presented.

Male mass was correlated with tarsus ($P < 0.001$), but was not significantly affected by the experiment ($P > 0.9$; Fig. 5). The interaction between year and the experiment was not significant ($P > 0.8$) and there was no significant difference between years ($P > 0.2$).

Female mass was correlated with tarsus ($P < 0.005$), and was significantly affected by the experiment

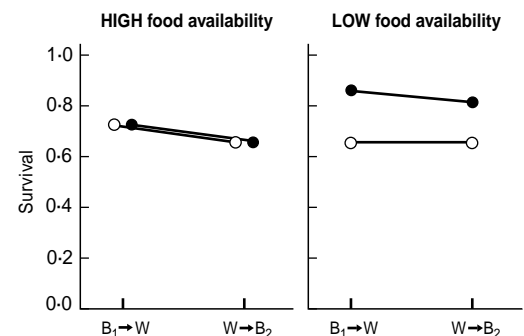


Fig. 4. Survival of control (○) and experimental (●) females from the breeding season until winter ($B_1 \rightarrow W$) and survival from winter until the next breeding season ($W \rightarrow B_2$) for years with high and low food availability in winter.

($P < 0.02$; Fig. 5). Experimental females had 0.5-g lower mass than control females (62% of the standard deviation of the overall mean). The interaction between year and the experiment was not significant ($P > 0.3$) and there was no significant difference between years ($P > 0.1$). Furthermore, there was no significant interaction between food availability in winter and the experiment ($F_{1,51} = 0.02$, $P > 0.8$).

Data of the sexes were pooled to investigate whether the experimental effect significantly differed between the sexes. In a multiple regression model that included year, sex, tarsus length and the experiment as a dummy variable, the interaction between sex and the experiment approached significance ($F_{1,113} = 3.4$, $P < 0.07$).

Discussion

Removal of second clutches enhanced the survival of females and their fledgling production in the next year. These effects were found in 2 years with low food availability in winter, but not in a year with high food availability in winter. In addition to this cost for the parents, the second clutch also had a negative effect on the reproductive value of the first clutch

(Verhulst *et al.* 1997). Long-term effects (i.e. 1 year later) of manipulations of reproductive effort on reproductive success have previously been recorded in a very limited number of studies (see Røskaft 1985; Gustafsson & Sutherland 1988).

The removal of second clutches to assess the costs of having a second clutch can be expected to lead to underestimation of the real costs, because the costs of laying and incubating the second clutch are ignored (Heaney & Monaghan 1995; Oppliger, Christe & Richner 1996). Furthermore, through clutch removal the costs of rearing a second clutch can only be measured for those birds that have chosen to lay a second clutch. The costs of rearing a second clutch could be different for those pairs that did not start a second clutch. Indeed, pairs may have refrained from starting a second clutch because the expected costs were larger.

The absence of an experimental effect on female survival in 1990 was attributed to the (higher) food availability in winter but it is possible that environmental quality was also better during the time that the second broods were reared. However, the number of fledglings from unmanipulated second clutches, which is assumed to be related to environmental quality, did not differ significantly between years with high and low winter food availability (high food availability in winter, 3.9 fledglings; low food availability in winter, 4.8 fledglings; $P > 0.1$). Nevertheless, the conclusion that the costs of rearing a second clutch depend on food availability in winter was based on a minimum number of years and it is obvious that this needs confirmation from more experimental work.

Male survival was not affected by the experiment, which is in contrast to the descriptive analysis of Tinbergen *et al.* (1985) where it was mentioned that results of their analysis were similar for both sexes. Experimental males produced more fledglings in the next year but this effect could be attributed to an effect on their partners. However, this still remains a cost of reproduction for the males. Furthermore, experimental males may have been in better condition in the next year (Gustafsson, Qvarnström & Sheldon 1995), and as a consequence have more extra-pair fertilizations in clutches of other females. In this way a cost of reproduction could have remained undetected.

The costs of rearing a second clutch differed significantly between the sexes (being higher in females). This implies that there will sometimes be a conflict between the sexes with regard to the decision to start a second clutch: there will be circumstances when it will be profitable for the male to start a second clutch, but not for the female.

CLUTCH SIZE AND MULTIPLE BREEDING

Manipulation of brood size of the first clutch affects the occurrence of second clutches (Tinbergen 1987; Smith *et al.* 1987; Lindén 1988; Verhulst 1995). A functional explanation of this result could be that the

Table 2. Manipulation of the second clutch and body mass (g) of roosting males and females in winter. Residual body mass was calculated separately for both sexes from a regression of mass on tarsus

Experimental category	Females					Males				
	Body mass		Residual Body mass		<i>n</i>	Body mass		Residual Body mass		<i>n</i>
	\bar{x}	SD	\bar{x}	SD		\bar{x}	SD	\bar{x}	SD	
1988 Control	17.7	0.8	+0.32	0.7	8	18.9	0.5	+0.21	0.3	11
1988 Removed	17.7	0.6	+0.22	0.6	9	18.8	0.9	-0.11	0.8	10
1990 Control	17.6	0.9	+0.05	0.8	8	18.4	0.8	-0.33	0.7	10
1990 Removed	17.2	0.7	-0.40	0.6	10	18.8	0.7	-0.04	0.7	10
1991 Control	18.0	0.8	+0.45	0.7	8	18.7	0.7	+0.13	0.6	12
1991 Removed	17.2	0.8	-0.35	0.7	13	18.7	0.7	+0.08	0.7	11

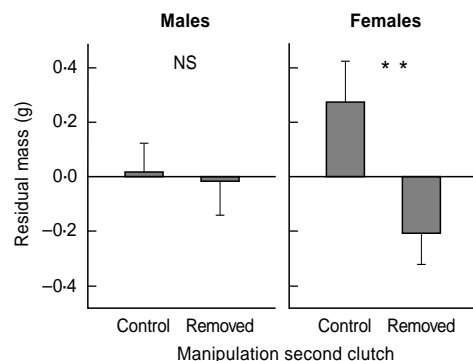


Fig. 5. Mass of roosting Great Tits in winter and reproductive effort in the preceding breeding season. Shown are the mean residuals (\pm SE) of a regression of mass on tarsus length. See Table 2 for sample sizes. NS not significant, ** $P = 0.01$.

costs of rearing a second clutch depend on the number of young in the first brood. No such effects were found however, but this may be due to the small sample sizes available to evaluate this point.

Manipulation of the number of young in the first brood did not have any detectable effects on parental survival or reproduction in the next year (Tinbergen & Daan 1990; Lindén 1990; Verhulst 1995). There are costs associated with rearing a second clutch (this study), which may have compensated for the (positive) effect of rearing, e.g. an experimentally reduced brood. This could explain the absence of effects of brood size manipulation on parental survival or reproduction in the next year, and indicates that the costs of a second clutch also plays a role in clutch-size evolution.

COSTS OF REPRODUCTION AND ENVIRONMENTAL QUALITY

Several authors have suggested that the costs of reproduction may depend on environmental quality (e.g. Tuomi, Hakala & Haukioja 1983; Reznick 1985; Bell & Koufopanou 1986; Roff 1992; Stearns 1992). A distinction can be made between the effect of environmental quality during reproduction and environmental quality between reproductive attempts because these situations may affect the costs of reproduction via different mechanisms. Furthermore, they may have different effects on the evolution of reproductive strategies since animals can adjust their reproductive strategy to the actual environmental quality during reproduction, but only to an expectation of environmental quality after reproduction.

What evidence is there for effects of environmental quality on the costs of reproduction, and are those effects of environmental quality during or after reproduction? It has been shown (Clutton Brock, Guinness & Albon 1983; Clutton-Brock, Albon & Guinness 1989) that the costs of reproduction in Red Deer *Cervus elaphus* were higher when environmental quality (population density and rainfall in August and September, which affects the grass stock available in winter) was low. However, it cannot not be ruled out that both rainfall and density had a direct effect on the phenotypic quality of females at the end of reproduction. A number of laboratory studies varied both reproductive effort and environmental quality, and concluded that the costs of reproduction were higher when environmental quality was low (Calow 1973; Calow & Woollhead 1977; Browne 1982; Feifarek, Wyngaard & Allan 1982). However, since environmental quality was kept constant during and after reproduction, these studies do not allow us to distinguish between effects of environmental quality during and after reproduction. This study, in conjunction with the study of Tinbergen *et al.* (1985), suggests that in the Great Tit the costs of reproduction depend on environmental quality between reproductive attempts. More experimental studies are needed to evaluate whether this is a general phenomenon.

In a stochastic environment, fitness does not only depend on the mean number of descendants, but also on the variance around the mean (Gillespie 1977). As a consequence, the optimal form of a decision rule in a stochastic environment is to 'bet-hedge' (Cohen 1966, 1967; Seger & Brockmann 1987). This implies that, when the optimal solution (e.g. one or two clutches) depends on the unpredictable quality of the environment, the optimal strategy is to make a second clutch in a certain proportion of cases, and to refrain from making a second clutch in the remaining cases. In the Great Tit, both costs (this study) and benefits (fledgling survival: Tinbergen *et al.* 1985) of second clutches depend on food availability in winter, and it seems likely that feeding conditions in winter cannot be predicted at the time second clutches are laid. This suggests Great Tits should bet-hedge with respect to the decision to start a second clutch.

MECHANISMS MEDIATING THE COSTS OF REPRODUCTION

Although experimental evidence is accumulating confirming the existence of costs of reproduction (reviewed by Reznick 1985; Bell & Koufopanou 1986; Lindén & Møller 1989; Dijkstra *et al.* 1990; Lessells 1991; Roff 1992; Stearns 1992), little is known of the underlying mechanisms. Both physiological (e.g. resistance to parasites, Sheldon & Verhulst 1996) and ecological (e.g. predation, Magnhagen 1991) processes could play a role. For example, rearing a second clutch may have resulted in an increase in somatic damage, which could affect the capacity to cope with environmental stress (e.g. adverse weather or disease). Somatic repair is easier to achieve when food availability is high (Nilsson, Källander & Persson 1993), and such a mechanism is therefore in accordance with the finding that the costs of rearing a second clutch depend on food availability in winter.

In the Great Tit, females, but not males, delay their moult when they start a second clutch (Tinbergen 1992) and thus females whose second clutch was removed may have speeded up their moult (Siikamäki, Hovi & Rätti 1994). This could affect their social dominance, because moult has been documented to interfere with agonistic behaviour, which in turn could lead to lower-quality territories in winter or reduced access to food. Such an effect could perhaps only appear in winters when food is scarce, since it seems plausible that even low-status individuals will obtain enough food in winters with high food availability. Furthermore, such a mechanism would also explain the difference between the sexes, because males are dominant over females.

Depletion of energy reserves could also be a mechanism mediating the costs of rearing a second clutch, but females had significantly lower mass in winter when the second clutch was experimentally removed

(Fig. 5). Assuming that this effect reflects a difference in energy reserves, this suggests that control females were in some way in less favourable conditions during winter because it is now generally thought that the optimal level of energy reserves is higher in adverse conditions (Houston & McNamara 1993; but see Verhulst & Hogstad 1996). Reduced time for moult has been suggested to result in plumage with lower quality with respect to insulation (Nilsson & Svensson 1996). The increase in energy reserves may therefore be an adjustment to increased energy requirements for thermoregulation, although experimental females may also have been in less favourable circumstances in other respects (e.g. social dominance, somatic damage or territory quality).

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